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THEORIES OF BIRD MIGRATION

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Migratory Route of the American Golden Plover

The American Golden Plover is known to travel in the neighborhood of 15,000 miles a year. Its breeding grounds are well within the arctic circle far beyond the northern tree line. In fact Gen. Greeley, the arctic explorer, found it nesting at 81° N. latitude within 600 miles of the north pole. These remarkable birds arrive in the far north about June 1st, remaining there approximately ten weeks. By the latter part of August, nesting duties completed, they have already traveled as far south as Labrador where a rich temporary feeding ground supplies them while the crowberries, common to that region, are ripening. From Labrador they move further south to Nova Scotia, and thence straight out over the open ocean 1,800 miles to the islands that lie east of Cuba and Porto Rico, sometimes breaking the journey at the Bermudas 800 miles south of Nova Scotia but more frequently passing by to the eastward. From the Eastern Antilles to the continent of South America is a flight of 600 miles more and after this mainland is reached they press on to the pampas region of Patagonia where they remain for the winter months, 8,000 miles from their nesting grounds. March finds them on the move again as far north as Guatemala and Texas. During April they are traversing the Mississippi valley, in May the vast territory of Canada, while early in June they are nest-building again in the land of the midnight sun, having completed the 15,000 mile circuit.

What explanation can be given to account for such astonishing behavior? How is a bird, who weighs only a few ounces and whose brain can easily be packed in a thimble, able to find its way over such vast reaches of land and sea, and what are the laws which impel it to carry out such a colossal undertaking in the face of all sorts of perils, not only once in a lifetime but every year so long as it lives? The American Golden Plover is an extreme case, but the laws which govern its behavior are doubtless the same as those which cause the lesser, but quite as noteworthy, migratory movements so generally observed among bird kind.

Early Mention of Migration

The migrations of birds have been recognized by man from the earliest times. Mention is made in the book of Job of the hawk that "stretches her wings toward the south." Homer observed the mighty rush of the water

fowl northward in the spring and Anacreon, in classic lines, welcomed the returning swallow five centuries before Christ.

Schlegel Serious attempts to ascertain the facts of migration in any detail have been attempted only within the last century. For instance in 1828 Schlegel of Haarlem made an analysis of the accounts of travelers in various lands upon 130 different journeys. After compiling all references which these travelers made to the birds which they saw he concluded from these heterogeneous statistics that, for any given locality, birds might be divided into three groups; first, *residents,* who remain all the year in one locality; second, *erratic wanderers,* who appear irregularly, and third, *migrants,* who pass through the locality at regular times. Since Schlegel's time there has followed many years of faunistic work by various observers who have catalogued the birds known to occur in different localities. This extremely useful kind of work is still being done in both hemispheres, since, until the general distribution of birds is more accurately known mere speculation upon their movements is productive of few results.

von Middendorf In 1855 von Middendorf of St. Petersburg combined all the faunistic data then available in an attempt to find out the manner of bird movements by means of what he termed isopeptic lines. The isopeptic lines were arbitrarily formed by connecting the points of first arrival of certain species over as large an area as possible for any one date. By constructing a series of such isopeptic lines upon the map of Russia for succeeding dates he obtained a graphic representation of the kind of advance made during migration, throughout that region, drawing therefrom the general conclusion that birds move forward during migration in a broad front. Furthermore, the direction of the main European migration routes he determined theoretically by extending lines at right angles to the isopeptic lines.

Sundevall and Peters It soon came to be seen, however, that only general results could be hoped for so long as particular instances were not known. The first attempt to obtain detailed data concerning the movements of any single species of birds was the outcome of a correspondence about the migration of storks begun during 1862 between Sundevall in Sweden and Peters in Berlin. These two naturalists called upon their colleagues to aid them in making observations at various localities. Thus in a short time a large amount of data was collected concerning the migratory movements of storks, a species particularly favorable for study by reason of their being so conspicuous and

everywhere well known. As the result of this collaboration, the migratory route of the stork in Europe has been established with considerable acuracy.

Palmen The efforts of Sundevall and Peters were followed in 1876 by the masterly work of Palmén of Sweden who determined the migratory route of nineteen species of European birds. Palmén emphasized the fact that birds do not travel in a "broad front" as suggested by von Middendorf but that instead each species moves in a definite path or route of its own.

Cooke About 25 years ago the U. S. Biological Survey began a systematic collection of data concerning the movements of migratory birds in North America and already several most valuable papers, based upon the abundant data thus being collected, have appeared from the pen of Mr. W. W. Cooke, who is in charge of these admirable investigations.

Meanwhile speculations have multiplied far in advance of facts. It goes without saying that satisfactory explanations of the laws governing bird migration can only be hoped for after a far greater basis of facts has been established. However, speculations and theories of bird movements, unsatisfactory as they are, possess a certain interest, not to say value, as indicating the progress of science along this line of investigation. These guesses at the truth may accordingly be grouped as the answers to two questions: first, how do birds find their way in migration, and second, why do birds migrate?

I. How do Birds Find Their Way in Migration?

Instinct Theory To say that birds find their way instinctively is only a roundabout method of acknowledging that we do not know what the mechanism of migration is. The term "instinct" is a vague generalization which, being made to apply to many diverse phenomena, loses its value in any particular case. Moreover the instinct theory not only does not explain anything but, since it does not admit of experimental test, closes the door upon the hope of ever reaching a satisfactory explanation of the phenomena to which it is applied.

Magnetism Theory In 1855 von Middendorf, to whom reference has already been made, advanced the novel theory that birds are guided by lines of terrestrial magnetism which cross in the body after some such fashion as in a solenoid. This speculation is interesting because there is no known fact whatever in support of it. There are, however, facts against it. In North America, for example, birds do not go toward the magnetic

pole as they appeared to von Middendorf to do in Russia. So far as I am aware there is among plants and animals no known case of response in any way to magnetic force.

Semi-circular Canal Theory

The attempt to locate some organ within the bird to which this function of path-finding might be referable resulted in the Mach-Breuer theory of the semi-circular canals which was elaborated particularly to explain how the carrier pigeon finds its way home. This theory rests upon the supposition that the semi-circular canals of the inner ear form an organ of equilibration by means of which an animal can orient itself in any of the three planes of space. Each of these three canals, which are situated at right angles to each other, enlarges at one of its ends into an ampulla, within which, surrounded by endolymphatic fluid, are located delicate nerve endings coming from the eighth cranial nerve. In whatever position the ear is held the endolymphatic fluid within the semi-circular canals presses more upon the nerve endings within one ampulla than upon those of the other two, and the particular stimulation thus received, upon being transferred to the brain, records for the animal its position in space. Along with this sensory registry of positions in space it is assumed that there has been developed the ability to record intervals of time upon the brain automatically. It is interesting in this connection to notice that the recognition of time intervals is a basic principle of music and birds are notably muscal. Besles a registry of position in space an of time intervals there may be developed a registry of the distance traversed in case a uniform speed is manitained. Thus when a pigeon going away from home travels at a given speed, for example, east twenty minutes, north thirty minutes and east again ten minutes, all these changes in direction, together with the time occupied in making them and consequently the distance traveled in following each direction, are recorded upon the brain as sounds are recorded upon the cylinder of a phonograph. To accomplish the return journey it is only necessary to reverse the record made upon the brain in order to get back to the starting point.

A theory of this kind has the advantage of being capable of exveriments to test its soundness, and such a test was made in 1893 by Professor Sigmund Exner in Vienna. Exner attempted to find experimentally whether the brain of the carrier pigeon records automatically the direction and distance taken in the outward journey in such a way as to be equipped to make the journey home. He first took two covered cages of pigeons several miles away from home to a locality unknown to the birds and out of

sight of all familiar landmarks. During the journey one cage, which was suspended on a wire, was rotated hundreds of times at every point where the direction of the route was changed, while the other cage, containing control pigeons, was borne with great care in order to introduce as little confusion in the stimuli received by the semi-circular canals as possible. When released at the journey's end one at a time so that they could receive no aid from seeing each other, Exner found that, out of the entire number, the first pigeon to arrive home was one that had been whirled! In further experiments Exner produced galvanic dizziness in half of his pigeons during the outward journey by means of a portable dry battery with which he repeatedly sent a slight galvanic shock through the ears. This operation causes a dizziness which is referable to a failure in the semi-circular canals properly to function. Thus in the case of his "galvanized" pigeons the semi-circular canals had been unable to make records with any completeness during the outward journey but, notwithstanding the fact, such pigeons found their way home as quickly as the control individuals which had not been so treated.

Finally, Exner narcotized pigeons in order to destroy their power of recording stimuli, with similar results. He accordingly concluded it is impossible so to confuse the sensory impressions received by a carrier pigeon upon its outward journey as to interfere with its ability to find its way home. Therefore, although the semi-circular canals undoubtedly assist very largely in equilibration and orientation as a mechanism to guide the homing pigeon they are inadequate and, taken alone, they certainly cannot account for the much more extensive journeyings of migrating birds.

Sense of Direction Theory

Certain investigators have attempted to attribute to migrating birds a sixth sense, namely of direction, without going into embarrassing details as to what the physical basis of such a supposed sense might be. It has been repeatedly noticed that animals other than birds have an apparent sense of direction. Everyone can tell, either from experience or hearsay, the uncanny way in which a cat, tied securely in a bag and taken ten miles away and deserted, is found on the doorstep waiting to be let in when its unappreciating master returns home. But seriously after all the discounts rendered necessary by the accounts of the nature fakirs have been made, there remains in the behavior of animals a considerable residue of fact which seems to have its only explanation in the assumption of a sense of direction.

An instance is given by members of the Harriman Expedition in Alaska of the remarkable flight of murres in a dense fog between Unalaska island and their feeding ground upon another

island about 60 miles away. These birds were seen repeatedly looming up in the fog behind the steamer then passing on ahead out of sight, flying as steadily and surely as if by compass although it was possible to see hardly more than a boat's length ahead. Such cases strengthen the conviction of many that there must be present in birds an unknown sense which serves them in some such way as the compass serves the mariner. This view, however, is hardly better than the instinct theory since it gives the answer to the problem in unknown terms.

The Landmark Theory

The landmark theory has rather more to recommend it. Exner came to the conclusion that carrier pigeons find their way home by seeing familiar landmarks and when such landmarks are not visible the birds explore until landmarks are found. This explains how his pigeons, whether whirled, galvanized or narcotized, were quite as well able to get home as those which had not undergone such interference with their sensory impressions upon the outward journey. Anyone who has observed swallows hawking for insects upon a summer afternoon or who has seen a hawk swoop down upon a field mouse from a dizzy height in the sky, must be convinced that the sight of birds is very acute. This is proven not only by their behavior but by anatomical evidence as well. The eye of the hawk is perhaps the most perfect optical instrument in nature. So far as the sense of sight goes it may be admitted that birds are well endowed to observe landmarks from a distance, while those birds that habitually migrate during the twilight, as nighthawks, bitterns, woodcock and certain sandpipers, being accustomed to feed at this time of day, have no difficulty in seeing objects in semi-light.

The objection must be raised to the landmark theory, however, that many birds do not follow river valleys, coast lines or mountain chains in the way they might be expected to do if they were guided by what appear to us to be the most obvious landmarks. Furthermore, migratory birds leave Cuba for Florida without hesitation upon cloudy nights when no landmarks are possibly visible and the stretch across the Gulf of Mexico, which is also regularly traversed by birds, is so great that even if migrants rose to a height of five miles, which is beyond reason, they could scarcely see one third of the way across to the other shore on account of the curvature of the earth. Sight alone, then, although it is an important factor, cannot be the only resource of the migratory bird.

The Follow-the-Leader Theory

Still another theory with a large element of probability in it may be briefly described as follows. Birds are social animals and fly in company with each other. The total migratory stream is a vast straggling army, spreading

out-or narrowing according to the character of the country over which it is passing. Dispersion over a wide area is the surest method of finding the way for in this manner a larger area of landmarks is visible to the migrating flocks. According to the best vantage point of vision, temporary leaders are continually created whom the others may follow. It is well known that when the leader in a harrow of wild geese becomes disabled the others are, for a time at least, thrown into confusion, showing that they were keeping to the path by following a leader. While certain species fly in comparatively close array, as cowbirds for example, others may be straggling far behind the pioneers so that all the members of any one species may occupy over a month in passing a given point. Thus it is possible for any individual bird to have companions constantly to guide it on its way when it might be unable to proceed independently. It is not necessary, however, to assume that the same birds are always the leaders in the flight or that the leaders themselves depend upon landmarks which they can see. It seems reasonable to believe that sound serves to keep the individuals of migrating hosts in communication with each other when sight fails for it is comomnly observed that bird-calls during migration are much more frequent upon foggy than upon clear nights.

In the case of carrier pigeons the successful individuals are those who have been trained over the course, that is, those who have learned the way either by seeing landmarks for themselves or by following a trained companion. There is no mysterious sixth sense of direction, no crossing of imaginary magnetic lines, no intricate automatic registry of distance and direction by means of the semi-circular canals. It is simply a case of a home-loving animal away from home putting its wits and senses and experiences together to get back to its home and in this case these known resources are sufficient for the task. Why may not this also be the true explanation of the manner in which birds find their way on those greater pilgrimages which we call migration? The murres flying in the fog, the migrants striking out from Cuba for invisible Florida or across the Gulf of Mexico toward an unseen shore, are all either traveling a course they have learned by experience or following within sight or call of others who know where to go. It does not seem any more impossible that a bird should learn to travel a familiar distance without landmarks than that a blind man is able to walk in a familiar path. What causes the migration movement is another problem entirely but, once given the incentive for this wonderful exodus, it seems reasonable to believe that the manner in which it is carried out, the way in which the path is fol-

lowed, may find an adequate explanation in the temporary leadership of some individual within sight or hearing of the others, who knows at least a fraction of the way by experience or who strikes out a safe path by means of landmarks.

Finally, it must be remembered that all who start upon this winged crusade do not reach the holy land. The annual loss of bird life during migration is unquestionably enormous. Birds are not driven by an unfailing instinct that carries them all automatically to their destination. The blunderers and the stupid ones are relentlessly eliminated in countless numbers. The more resourceful ones, the quicker witted, the more vigilant, accomplish the grand tour amid perils innumerable with many a hair-breadth escape and the survivors are those choice spirits who, having thus won their spurs by noble effort, or because they possess the birthright of a superior endowment over their fellows, become the ancestors of other birds. So it is that winning qualities are engrafted upon the race by hereditary transmission. It is to be greatly wonderel at that, after ages of such rigid selection, we should at last have birds to-day whose performance is so remarkable that we are tempted to attribute it to powers uncanny and unknown?

II. Why Do Birds Migrate?

Theories to Account for the Fall Migration

Having discussed some of the theories advanced in explanation of how birds find their way during migration let us consider some of the reasons which have been given to solve the origin of the migration habit. Why do birds migrate at all? At once it is seen that the fall migration seems to present fewer difficulties than the spring migration.

The Temperature Theory

It has been maintained by some investigators that the approach of cold weather causes birds to go south in the fall and it is quite true that if all birds attempted to remain in northern latitudes during the winter many would doubtless succumb to the cold. The main factor in such a disaster, however, would not in all probability be low temperature in itself but rather scarcity of food dependent upon low temperature during the winter months. The fact that there are repeated instances of birds, such as robins, song sparrows, etc., which ordinarily migrate south, remaining occasionally in their summer habitat throughout the entire winter, demonstrates that these birds are able to endure low temperature when they have a plentiful food supply. In this connection two well known facts are significant. First, the ordinary bodily temperature of a bird is always several degrees warmer than in the case of man, and secondly, the fall migration begins and is largely completed before the weather becomes cold.

The Premonition Theory Years ago Brehm attempted to account for the fall migration by assuming that birds have premonitions of severe weather, or in other words that they are endowed in some mysterious way with a meteorological sense. This theory, which at first thought seems entirely fanciful, in reality contains a large element of probability but not exactly in the way that Brehm intended. Birds with their large lungs, pneumatic bones and numerous internal air sacs, are, to a remarkable degree, living barometers, responding with great delicacy to changes in barometric pressure. The uneasy behavior of robins and the repeated calls of cuckoos before a storm are familiar illustrations of this fact. That birds can anticipate winter, however, and as a result make an effort to avoid its disastrous effects, is beyond demonstration and seems quite unlikely.

The Short Day Theory Another alternative has been suggested, namely, that toward the fall of the year the days become too short for the bird to complete its daily task of feeding. When the enormous activity of birds is brought to mind and one remembers how rarely a resting bird is seen, particularly among seed and insect eaters, the hardship resulting from shortened working hours can be readily appreciated. The migration south, however, begins before the days are perceptibly shorter and so this theory suffers, as does many another, because of a few obtrusive incontrovertible facts!

The Food Supply Theory Still other theorists have assumed that the factor of greatest importance in causing the fall migration is a diminished food supply but here again it must be admitted that a large per cent. of migrating species leave for the south in the very height of the seed and insect harvest. It may be pointed out, however, that upon the ground of food supply, natural selection would promptly eliminate those who did not go south and would tend at the same time to favor the perpetuation of those who varied in the direction of southern migratory habits, whatever the cause of those variations might be.

Theories to Account for the Spring Migration Turning now to the spring migration, the factor of food supply seems to be of much less immediate importance since in many cases birds, as for instance the water fowl, push their way out of a land of plenty into a region of scarcity.

The Instinct Theory That it is a bird's *instinct* to go north in the spring is no better an explanation of the origin of migration than it is of how a bird finds its way during migration.

The Homesick Theory Another attempt at an explanation is based upon the fact that in the spring migration birds are returning home to the place where they were born. May it not be then that they are overtaken by a strong desire to revisit their birthplace as the changing seasons duplicate the climatic conditions which existed when they formerly dwelt there? May they not be driven by a kind of home-sickness to fly north to the scenes of their early life? This is a favorite theory with those who are accustomed to endow birds with semi-human attributes upon a sentimental rather than upon any anatomical basis. The theory suffers somewhat when it is remembered that most birds forsake the home they make such strenuous endeavor to revisit, the moment their nesting duties will allow which would hardly be expected if they possessed such an overmastering affection for a particular locality as the homesick theory implies.

The Desire to Disperse Theory Again, to say that birds have a "desire to disperse" in the spring of the year, as Dixon suggests, simply begs the question as to what actually causes the dispersal.

The Nestling Food Theory Alfred Russel Wallace, whose biological opinions are certainly entitled to respect, points out that the food upon which many nestlings are fed consists of soft bodied insects and other materials that become relatively rare in the tropics during the dry season. It is so customary to think of the tropics as a region continually teeming with all sorts of life that testimony to the contrary by one who has spent many years there, comes at first as a surprise. It is, however, undoubtedly true that food of a quality suitable for nestlings would not be present in sufficient quantity if all the migratory species remained there to nest. Consequently in this sense, the spring migration may primarily depend upon food supply. Omnivorous birds whose food supply is to a lesser extent affected by the changing seasons, migrate less than those who feed upon a restricted diet.

The Safe Nesting Site Theory Another theory has been presented by Professor Brooks of Johns Hopkins University, namely, that birds go north in the spring in order to find safer nesting sites than are available in the over populated tropics. It is natural that all animals during the breeding season should seek retirement and a place of security in which to rear their young and this seems to be the universal rule among all those animals which in any active way care for their offspring. But is it a fact that there are more safe nesting sites in the north than in the tropics? Surely in the luxuriant tropical vegetation there are more nooks for concealment, acre for acre, than in our open

northern forests! In both regions only a small number of the sites available for nesting are utilized. If the reason for nesting in the north was for increased safety it would be expected that those birds which do remain behind to contend with the perils of tropical nesting, would develop greater skill in building nests inaccessible to enemies than those going north who would presumably be exposed to fewer perils. Such, however, is by no means the case. Tropical nests cannot be distinguished from northern nests by any such criterion of efficiency against enemies. Some of our best nest builders, the Baltimore Oriole for example, are also notable migrants. In the case of both of these latter theories it would seem as if Nature, who always works along the lines of least resistance, would have found it easier to adapt migrating birds to a different sort of nestling food or to perfect in them the skill necessary to build securer nests in the tropics before evolving the intricate machinery incident to annual migration.

The Vacuum Theory

A theory proposed by Allen seems more reasonable. It rests upon the idea that "Nature abhors a vacuum" and, therefore, any accessible territory from which animals have been temporarily excluded will not long remain unpopulated after the cause of temporary banishment has been removed. During the winter birds are forced to abandon the northern latitudes for the tropics because of cold and the consequent shortage of food. When spring comes this entire vacated area is again thrown open for habitation at the very time when the birds, temporarily crowded into the tropics, are beginning to seek nesting places. It is quite as inconceivable to imagine that birds, with their active powers of flight, should fail to reinvade the territory, from which they had been temporarily driven by winter, as soon as it is again available for habitation, as that an expansible gas should remain in a flask after the stopper which confined it there had been removed. This theory, then, explains spring migration as a logical expansion consequent upon the compression into the tropics during winter of a large per cent. of the bird population of all latitudes.

The Over-population Theory

Another factor has been emphasized by Taverner. This may be called the over population theory depending as it does upon the circumstance that whenever the breeding season opens there is suddenly a great increase in population within a given feeding area. Such a condition must result in a keener competition for food and those birds who are stronger or who are the earliest to mate and produce young drive out the weaker and tardier ones into the surrounding region. This dispersion would not be towards the south, neither toward the east nor the west, because in

all these directions the territory would be equally preempted, but rather toward the north where there are fewer birds. Thus migration from the tropics might have had its origin. The direct result of such a movement would be that those individuals that were forced to become explorers in search of an adequate food supply would come to a halt only when compelled to do so by lack of food or when harrassed by superior competitors or, finally, by the demands of that period in their life cycle when the physiological impulse to nest-building can be no longer delayed.

Taverner explains the fall migration in the same way. That is, an overpopulation occurs in the nesting region at the north. The old birds drive away the young ones, or the first nestlings to mature become better established than those hatched later, driving the latter out. These being thus forced to migrate, on account of unfavorable conditions in the north find relief only by moving south and this constitutes the fall migration. This theory assumes that it is among weaker birds, those unable to hold their own, that the wonderful and complex habit of migration has developed, a habit demanding apparently far greater qualities of courage, persistence and resourcefulness than would be required by competition for a livelihood with their fellows in a neighborhood already familiar to them.

Ancestral-Habit Theories

All of the theories thus far mentioned to explain migration, namely, instinct, homesickness, dispersal, quality-of-nestling food, safe nesting sites, vacuum and overpopulation, seek to find an explanation in factors now operative. It is possible that a key to the puzzle may be found by regarding the performance as an inheritance of habit whose origin depends upon factors which have now ceased to act.

Graser's Theory

One of the most recent theories embracing this point of view was proposed in Germany by Gräser in 1904 and is based upon the supposition that the ancestors of modern birds, living in Tertiary times were very vigorous flyers who passed freely from one Tertiary island to another across immense stretches of water in order to find food and nesting sites. As the widespread tropical environment of the Tertiary times gave place to modern climatic conditions with changing seasons, and, as the present distribution of land and water gradually developed from the immense Tertiary seas with their numerous islands, birds more and more found suitable conditions of life in restricted areas wandering less and less until finally these ancestral wanderings have become limited to the regular fall and spring migrations, while many species are practically stationary. The logical conclusion of Gräser's theory is that birds are constantly becoming less

migratory and in time will become so well adapted to local conditions that migration will cease. This bold conception of the case loses significance when it is remembered that all the evidence from embryology, comparative anatomy and palaeontology points unmistakably to the conclusion that birds have arisen from reptile-like ancestors of the crawling or lizard type and not from the flying or pterodactyl type, and, moreover, that the art of flying was a gradual acquisition which had by no means reached the perfection in Tertiary times which Gräser's theory presupposes.

The Deichler-Jäger Theory

Another ancestral-habit theory, known as the Deichler-Jäger theory after its proposers, lays particular emphasis upon the rôle played by the glacial period toward the end of Tertiary times. There is geological evidence that during the pleistocene period at least three distinct glacial ages occurred one after the other, during which the present temperate regions of the earth were slowly invaded by an encroaching polar sheet of ice until they became quite uninhabitable except by arctic organisms. Before and between these glacial ages modern temperate regions swung to the tropical extreme in character which is proven by the discovery of fossil ferns as far north as Greenland. The Deichler-Jäger theory assumes that birds as a class in all probability arose from reptile-like ancestors during Tertiary times and that their original home was in the north. So long as the climate remained essentially tropical throughout the year there was no occasion for deserting this area. With the gradual advent of the first glacial age, however, the climate of the north slowly changed from being tropical the year around to a condition of seasonal changes somewhat similar to that obtaining today. When these seasonal changes became extreme tropical conditions were interrupted and the first winter occurred. There is no reason to believe that this first winter was either sudden or severe but, in the course of time, it became an established annual occurrence and was finally much more severe than our winters at present, as has been demonstrated by the occurrence of fossil reindeer bones in France and arctic musk-oxen as far south as Kentucky.

Now when organisms of any locality are overtaken by winter one of these results may occur; first, they may simply perish; second, they may hibernate through the cold weather in a semi-torpid condition, or finally, they may migrate to a more favorable environment. Birds, being endowed with the power of locomotion through the air pursued the latter alternative and thus the fall migration had its origin. Every spring as the advance of the glacial sheet relaxed for a season the birds which had been driven south into crowded quarters by the rigors of winter temporarily

reoccupied the ground they had lost, and these annual oscillations becoming greater and greater as the glacial age gradually gave way to an interglacial or post-glacial age, the conditions of migration which we observe today became established by long repeated practice.

The Dixon-Braun Theory A third ancestral-habit theory was developed independently in 1900 by Braun, who observed migrating birds extensively for several years in Constantinople and in 1892 by the English ornithologist, Dixon. The Dixon-Braun theory postulates that the center of distribution of birds, that is, their original home as a class, was not in the north as the Deichler-Jäger theory assumes, but in the tropics. The reason for this conclusion lies in the fact that many genera of our migratory birds are most largely represented by tropical species which do not migrate at all. For example, there are many more species of flycatchers remaining throughout the year in the tropics than migrating north, indicating that the original distribution-center from which flycatchers in general have spread must have been in the tropics where they are now most at home. As a result of overpopulation or famine in times past these tropical birds have been forced to travel to less crowded and more favorable localities for food. Relief could be found only toward the north since overpopulation is most likely to occur during the spring breeding season at a time when the northland is just released from the rigors of winter. Thus, according to the Dixon-Braun theory the first migration was a spring migration while according to the Deichler-Jäger theory the first migration was a fall migration. The Dixon-Braun theory further supposes that the original spring migrants, having been forced north by over-population are in turn compelled as winter comes on to retreat south into the overcrowded tropics or perish, only to repeat the experiment of finding relief in the north as soon as the advent of spring allows. In this way the old birds perform again what in their experience had proved to be a successful experiment, while the young birds go along with them and learn the habit.

The Kobelt-Duncker Theory A recent attempt has been made by Duncker in Bresslau (1905) to combine elements of the two theories last mentioned. Duncker accepts the classification of birds made by Kobelt (1902) into *summer-excursionists* (Sommerfrischler) and *winter-wanderers* (Winter fluchter). The former are birds whose home was originally in the south but who now make an annual excursion (Badereise!) north in order to breed returning home again as soon as this function is accomplished, while the latter comprise those whose home was always in

the north and who are temporarily driven abroad in the fall by stress of temperature and lack of food, only to return home again as soon as physical conditions allow. The summer excursionists go into a foreign land far away from their ancestral home or point of origin as a species, to perform the highest act of their lives, that is, the production of offspring. The winter-wanderers breed, as good conservatives should do, upon their ancestral acres but are obliged to be wanderers therefrom during many months of the year.

The Marek Theory

In the Ornithologisches Jahrbuch for 1906 there appeared still another theory to explain why birds migrate. It was put forward by Professor Marek of Hungary and emphasizes the factor of barometric pressure as being of the greatest importance in determining the migratory movements of birds. Marek's conclusions are entitled to serious consideration for they are based upon many years of painstaking investigations concerning the correlation between bird migration and barometric conditions. He began by comparing known migrations of the woodcock in Europe with the weather charts of the same dates and found that, aside from minor deviations, these birds migrate from anti-cyclonic areas of high barometric pressure to cyclonic areas of low barometric pressure. This coincides in general with the direction of the wind but Marek would not say that it is the wind which causes the movements of birds,—rather that both wind and migration are caused by the same conditions, namely, the proximity of two areas of unequal barometric pressure. During the winter the polar regions form an anti-cyclonic area of high barometric pressure with low temperature and clear air relatively free from moisture while in the tropics there is a corresponding area of low barometric pressure with high temperature and much humidity. The prevailing winds are from the north because the air always flows "down hill" from high pressure areas to those of low pressure. When spring comes there is a relative shifting in position in the barometric maxima and minima. In the north the temperature rises, humidity, cloudiness and precipitation all increase and an area of low barometric pressure becomes gradually established while the reverse conditions are occurring in the south. The result is that southerly winds become the prevailing ones and, at the same time, birds who are extremely sensitive to barometric changes unconsciously begin their spring migration. In the same way the fall migration is initiated by the shifting of the barometric maxima and minima.

Irregularities in migration, such as remarkable flights of birds

and unusual delays in the migration movement are all directly traceable to the barometric conditions prevailing at the time.

Marek's observations begun upon the woodcock were extended to very many other species. In fact, the paper referred to is a summary and generalization of 43 papers bearing upon migration, which this industrious investigator has published. It must be admitted that Marek's theory has the great advantage of dealing with known factors which may be made the object of further investigation. From his point of view there is no necessity for referring the habit of migration to hypothetical ancestral behavior, nor for endowing birds with such human attributes as love of home or the memory of previous successes. The streaming northward of birds in the spring and their return southward in the fall are both primarily dependent upon the same observable external factors as those which cause the flow of the air in the form of prevailing winds, northward in the spring and southward in the fall

Conclusion

Yet the riddle has by no means been solved. There still remains an immense halo of mystery around bird migration because there are so many things we do not know. We not only do not know *why* birds migrate but as yet we do not know *how* they migrate except in a general way.

What becomes, for instance, of the swallows, has been a conundrum for 2,000 years. Aristotle thought that swallows passed the winter buried in mud or in the bottom of ponds. Linné credited the hibernation idea. Dear old Gilbert White, in spite of his observing eye, died in doubt. Finally, a few decades ago an Italian naturalist thought it worth while to submerge a few swallows under water to see how long they would survive. These feathered martyrs to science of course promptly died, and thus at least there was delivered the death blow to the hibernation-under-water theory, but to this day no one knows the complete migratory route of the swallows nor where they pass the winter. Mr. Wells W. Cooke, our American authority upon bird migration, writes: "Upon leaving the Gulf of Mexico did they drop into the water and hibernate in the mud as was believed of old, their obliteration could not be more complete."

The meagerness of our knowledge concerning the migration of swallows is repeated to a large extent in the case of almost every other species when we seriously attempt to winnow out fact from fancy. It may, therefore, be said in conclusion that, until the store of facts as to how birds migrate has been greatly increased, we can only delight ourselves with interesting speculations as to *why* birds migrate, acknowledging the problem unsolved.